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A New Species of *Saxicavella* (Bivalvia: Hiatellidae) from California with Unique Brood Protection

by

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Abstract. A relatively common central and southern California infaunal bivalve species, *Saxicavella* ***nybakkeni*** Scott, sp. nov., is described. Significant siphonal, mantle, and reproductive differences between *Saxicavella* and other members of the Hiatellidae necessitate the erection of a new subfamily, **Saxicavellinae** Scott, subfam. nov.

INTRODUCTION

Small, infaunal bivalves composing the genus *Saxicavella* Fischer, 1878, have long presented vexing problems to malacologists. My introduction to the poorly understood genus *Saxicavella* came during a visit to the Natural History Museum of Los Angeles County (LACM) where I was shown several specimens of a new bivalve species from southern California that were tentatively placed in the genus *Paramya* Conrad, 1860 (Myidae). The shell was reminiscent of a very small *Panomya* Gray, 1857, but the animal lacked siphons.

I thought little about the LACM specimens until I received an inquiry from Michael Kellogg of the San Francisco Bureau of Water Pollution Control in 1989. He suggested the possibility of sexual dimorphism in *Saxicavella pacifica* Dall, 1916, based on specimens of *Saxicavella* obtained off San Francisco. Two forms had been sampled sympatrically, one elongate and slightly flaring, fitting Dall's original description of *S. pacifica,* and the other shorter and broadly flaring.

During sorting of live samples collected by epibenthic sled during the 1991 Moss Landing Marine Bivalve Workshop, several specimens of the LACM "*Paramya*" (which proved to be equivalent to Kellogg's short, broad *Saxicavella*) were found. I seized the opportunity to study this perplexing bivalve, and was pleased to learn that it was especially hardy in laboratory conditions.

During subsequent discussions with Don Cadien of the Los Angeles County Sanitation District Marine Biology Laboratory and other members of the Southern California Association of Marine Invertebrate Taxonomists, I learned of *Saxicavella* specimens with possible external broods. Upon examination of these specimens I determined that two species of *Saxicavella* are present in California, and both utilize a previously unrecorded form of larval brood protection.

This paper erects a new subfamily for *Saxicavella,* provides additional information on the living animal, describes a new species of this genus from California, and documents a previously undescribed form of brood protection in bivalves.

MATERIALS AND METHODS

Seven live specimens of *Saxicavella* were collected off Moss Landing in Monterey Bay, California, by the R/V *Ricketts* at 31 m and 60 m depth using an epibenthic sled.

Individuals were live sorted from bulk sediment samples and maintained in running seawater at approximately 9°C for over 10 days with no sign of reduced activity. Live

specimens were placed in a glass dish of seawater and native sediments from the sample site. Crawling and burrowing activities were observed using a dissecting microscope. Active animals were also examined apart from the substrate, allowing a better view of the mantle, siphonal region, and foot.

In one specimen, the right valve and mantle were removed, and ciliary currents and organs of the mantle cavity were examined. Specimens were then relaxed for 18 hours in an isotonic solution of magnesium chloride and seawater (72 g $MgCl_2$/L). Following relaxation, specimens were fixed in 5% formalin and after two days transferred to 70% ethyl alcohol. Two specimens were prepared utilizing standard histological procedures at the Department of Zoology, University of Hong Kong, and were transverse sectioned at 6μm. Alternate slides were stained with either Ehrlich's hematoxylin and eosin, or Masson's trichrome.

Abbreviations of institutions mentioned in the text: BMNH, The Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; LACM, Natural History Museum of Los Angeles County, California; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts; MLML, Moss Landing Marine Laboratory, California; SBMNH, Santa Barbara Museum of Natural History, California; USNM, National Museum of Natural History, Washington, D.C.

SYSTEMATICS

Superfamily Hiatelloidea Gray, 1824

Family Hiatellidae Gray, 1824

[= Saxicavidae Swainson, 1835]

Subfamily **Saxicavellinae** Scott, subfam. nov.

Type genus: *Saxicavella* Fischer, 1878.

Diagnosis: Shell less than 15 mm, thin, with only commarginal striae; inequilateral, posterior end longer; hinge plate reduced, small posterior cardinal tubercle may be present in both valves; ligament posterior, very small, attached to a nymph. Siphons very reduced or absent, mantle fusion not complete ventrally (Type B of Yonge, 1957). The type genus is the only recognized member of this subfamily.

Yonge (1971) listed no less than six major differences between *Saxicavella* and other members of the Hiatellidae but continued to place it with other members of the family. The short or absent siphons, incomplete mantle fusion and heteromyarian condition provide ample characters to place *Saxicavella* into a new subfamily. Whereas *Hiatella, Panomya, Cyrtodaria,* and *Panope* have developed siphons, complete fusion of periostracal secreting surfaces of the inner surface of the outer mantle fold (Type C of Yonge, 1957), and are isomyarian, they are therefore retained in the subfamily Hiatellinae.

Saxicavella Fischer, 1878

Type species (monotypy): *Mytilus plicatus* Gmelin, 1791, *ex* Chemnitz MS, of Montagu, 1808 [ICZN Code Article 70c, deliberate misapplication of name], = *Saxicavella jeffreysi* Winckworth, 1930 [a new species based on Jeffreys, 1865:75–77, not a new name as stated].

Description: Shell small (<15 mm); elongate to rhomboidal; inequilateral, posterior longer; posterior end flaring, height of anterior end much less than posterior; slightly to widely gaping; pallial sinus absent. Hinge plate reduced, with only a sunken nymph posterior of beaks; cardinal teeth absent in adults. Siphons absent or greatly reduced, inhalant opening may have short lip.

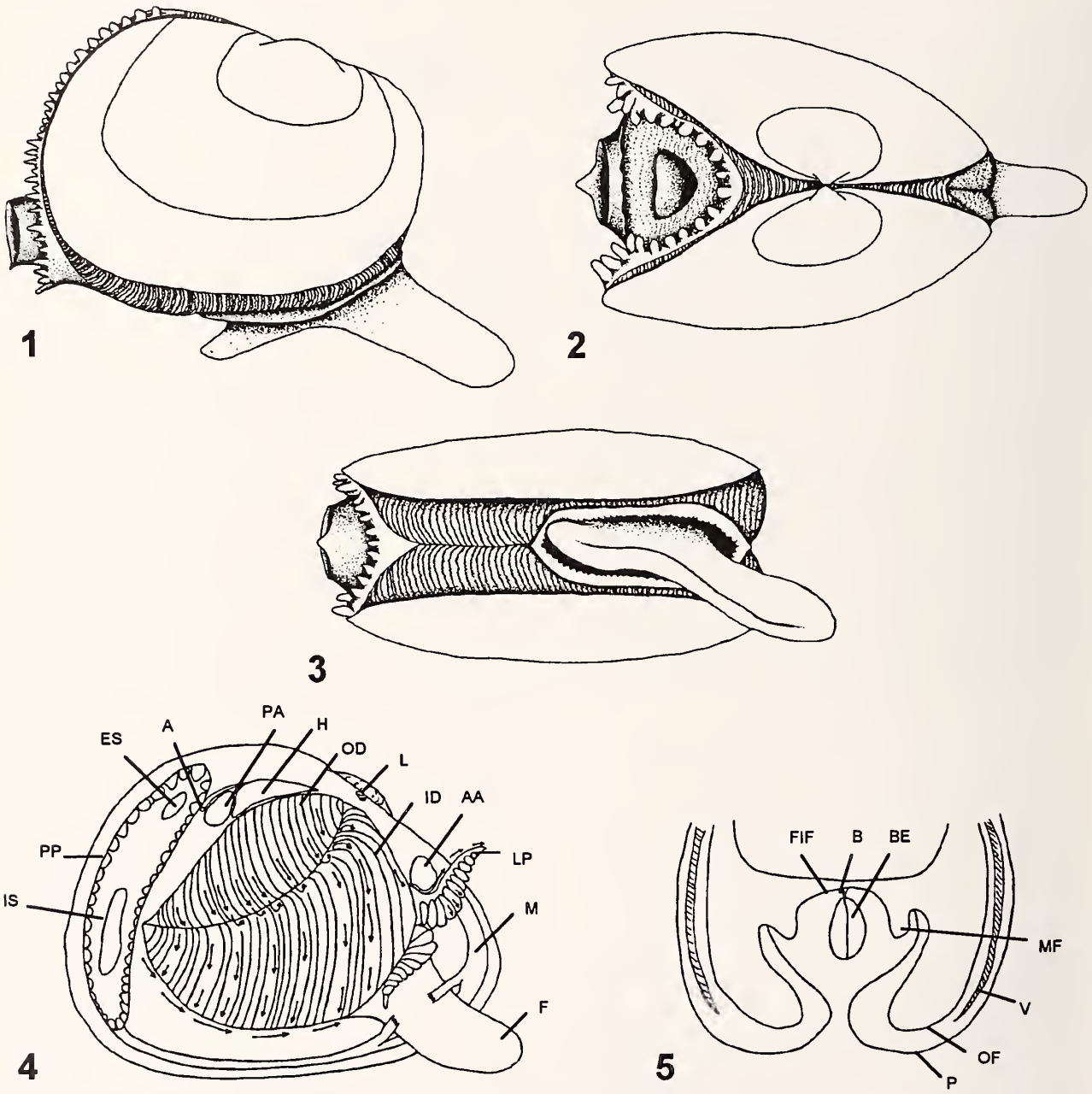
Discussion: Montagu (1808) first recorded and described a member of *Saxicavella* from the North Atlantic which he had been shown by J. Laskey and incorrectly assigned it to *Mytilus plicatus* "Chemnitz, 1785," from the Nicobar Islands, Bay of Bengal, India. Because Chemnitz (1785) is an unavailable work, this name is first made available in Gmelin, 1791, *ex* Chemnitz MS. Although Montagu did not include an illustration, his description of the shell adequately documents the small, broadly flaring species from Scotland and hinted that it might be a new species. Laskey (1811: pl. 8, fig. 2) provided an illustration of the specimen examined by Montagu.

Subsequent workers placed "*Mytilus plicatus*" of Montagu in widely separated families including the Hiatellidae (Turton, 1822), Psammobiidae (Jeffreys, 1847), Lyonsiidae (Gray, 1851), and Myidae (Weinkauff, 1866).

Forbes & Hanley (April 1848:149) extensively described and illustrated this species as juvenile *Saxicava rugosa* Linnaeus, 1767, but later stated in their appendix (Forbes & Hanley, 1852:248) that it was probably a new species. Jeffreys (1865) provided additional descriptions of "*Panope plicata* Montagu" and suggested possible synonyms that are now thought to belong in the Myidae and Corbulidae.

Fischer (1878) recognized the species as belonging to a distinct genus and erected *Saxicavella* for it. Lamy (1924) documented the details of the unstable placement of *S. plicata* (Montagu), but the type species of *Saxicavella* did not have a valid name until Winckworth (1930) proposed *S. jeffreysi,* some 122 years after Montagu's original description of the species.

As Winckworth did not designate a type specimen for *Saxicavella jeffreysi,* I hereby designate a **lectotype** from the Jeffreys collection in the U.S. National Museum of Natural History (USNM 171581, length = 9.0 mm, height = 4.9 mm, 1 right valve; Figure 6). The lectotype is a specimen figured by Jeffreys (1865, pl. 3, fig. 2, right specimen). Additional paralectotypes figured by Jeffreys are found in the following lots: USNM 878921 (Jeffreys 1865, pl. 3, fig. 2, left paired specimens) and USNM 171580 (Jeffreys, 1869, pl. 51, fig. 1). There was no precise locality associated with the Jeffreys material, but because



Explanation of Figures 1 to 5

Saxicavella ***nybakkeni*** Scott, sp. nov. Figures 1–3. Holotype in life (SBMNH 140090; length 5 mm; height, 3.5 mm; width, 4 mm). Figure 1. Lateral view as seen from the right side. Figure 2. Ventral view. Figure 3. Dorsal view. Figure 4. Organs and ciliary currents of the mantle cavity as seen from the right side with shell and mantle removed. Figure 5. Diagrammatic representation of a transverse section through the mantle, taken just posterior of the pedal gape. Key: A, anus; AA, anterior adductor muscle; B, byssus; BE, brooded embryo; ES, exhalant siphon; F, foot; FIF, fused inner mantle folds; H, heart; ID, inner demibranch; IS, inhalant siphon; L, ligament; LP, labial palp; M, mantle; MF, middle mantle fold; OD, outer demibranch; OF, outer mantle fold; P, periostracum; PA, posterior adductor muscle; PP, posterior papillae; R, rectum; V, valve.

he does mention a variety of locales around the British Isles, there is no doubt the specimens are from the northeast Atlantic Ocean.

Saxicavella ***nybakkeni*** Scott, spec. nov.

Figures 1–5

Description: Shell small (to 10 mm length, SBMNH 43802), thin, white, semi-transparent; rhomboidal, posterior end greatly expanded, anterior broadly rounded; inequilateral, posterior end much longer; surface uneven, rough, with uneven commarginal striae; valves widely gaping on all borders, only joined at beaks (width in life nearly equals length); beaks small, broad, not prominent; ligament small, not protruding, attached to small deeply sunken nymph just posterior of beaks; hinge plate narrow, without cardinal teeth.

Mantle thick, fleshy, expanded past shell margins in life, completely fused on all but ventral margin (Figures 1–3). Siphons very reduced; inhalant aperture with a very short, thin siphon with a sharply pointed ventral projection; exhalant siphon short, thick, dome-shaped with a narrow aperture. Posteriorly, stout papillae form a continuous lateral fringe along the shell margin.

Foot long, slender with short heel; byssal groove long, extending to the beginning of the heel. The organs and ciliary currents in mantle cavity are illustrated in Figure 4. Inner mantle folds and inner surface of middle mantle folds fused (Type B of Yonge, 1957; 156–157) except at pedal gape (Figure 5).

Type material: Holotype SBMNH 140090; dimensions, height-3.5 mm, length-5.0 mm; paratypes SBMNH 140091, plus others deposited at LACM, USNM, BMNH. All types preserved in 70% ethyl alcohol.

Type locality: United States, California, Monterey County, Monterey Bay, off Moss Landing; 36°48.7′N, 121°48.6′W; 31 m. Paratypes from 36°50.2′N, 121°51.7′W; 60 m.

Distribution: San Francisco (CAS) to Santa Monica Bay (SBMNH), California; 31–61 m.

Etymology: This species is named after Dr. James Nybakken of Moss Landing Marine Laboratory, who has consistently added to the knowledge of California marine mollusks and has motivated many students to pursue careers in malacology and marine biology.

Comparisons: The only other eastern Pacific species, *Saxicavella pacifica* (Figure 7), is more elongate and has a much smaller gape posteriorly than *S.* ***nybakkeni.*** *Saxicavella pacifica* also has a distinctly protruding ligament on a shallow nymph, compared to the small, non-protruding ligament of *S.* ***nybakkeni*** which is attached to a deeply sunken nymph.

The closest species to *Saxicavella* ***nybakkeni*** in external shell morphology is *S. sagrinata* Dall & Simpson, 1901, from the Caribbean (Figure 8). The external shell surface of this species has minute granules compared to the roughened, non-granular *S.* ***nybakkeni.*** *Saxicavella sagrinata* has narrow, pointed beaks, a small posterior cardinal tubercle, and a shallow nymph, unlike the broad beaks, lack of cardinals, and deeply projecting nymph in *S.* ***nybakkeni.*** The anatomy of the Caribbean species is unknown.

Living animal: When placed on its side in a petri dish with native soft sediment and cold seawater, the animal extends its foot down into the substrate and pulls itself vertically; the foot then immediately digs further into sediment and draws the animal further into the substrate. It is a very active crawler. The foot appears to produce a thick mucus that allows it to attach to substrate and obtain purchase. A very thin, clear byssus is also secreted.

While in an upright crawling position, the animal pushes the anterior end into the substrate, the foot then pulls anteriorly into the substrate while moving forward, forming a trough in the sediment. Maintaining a vertical orientation, the animal burrows forward into sediment (with valves opening and closing while burrowing) until only the posterior end is visible. The inhalant siphon is frequently covered with coarse sediment. The burrowing sequence in the laboratory, from horizontal to completely buried and at rest, took 4.5 minutes.

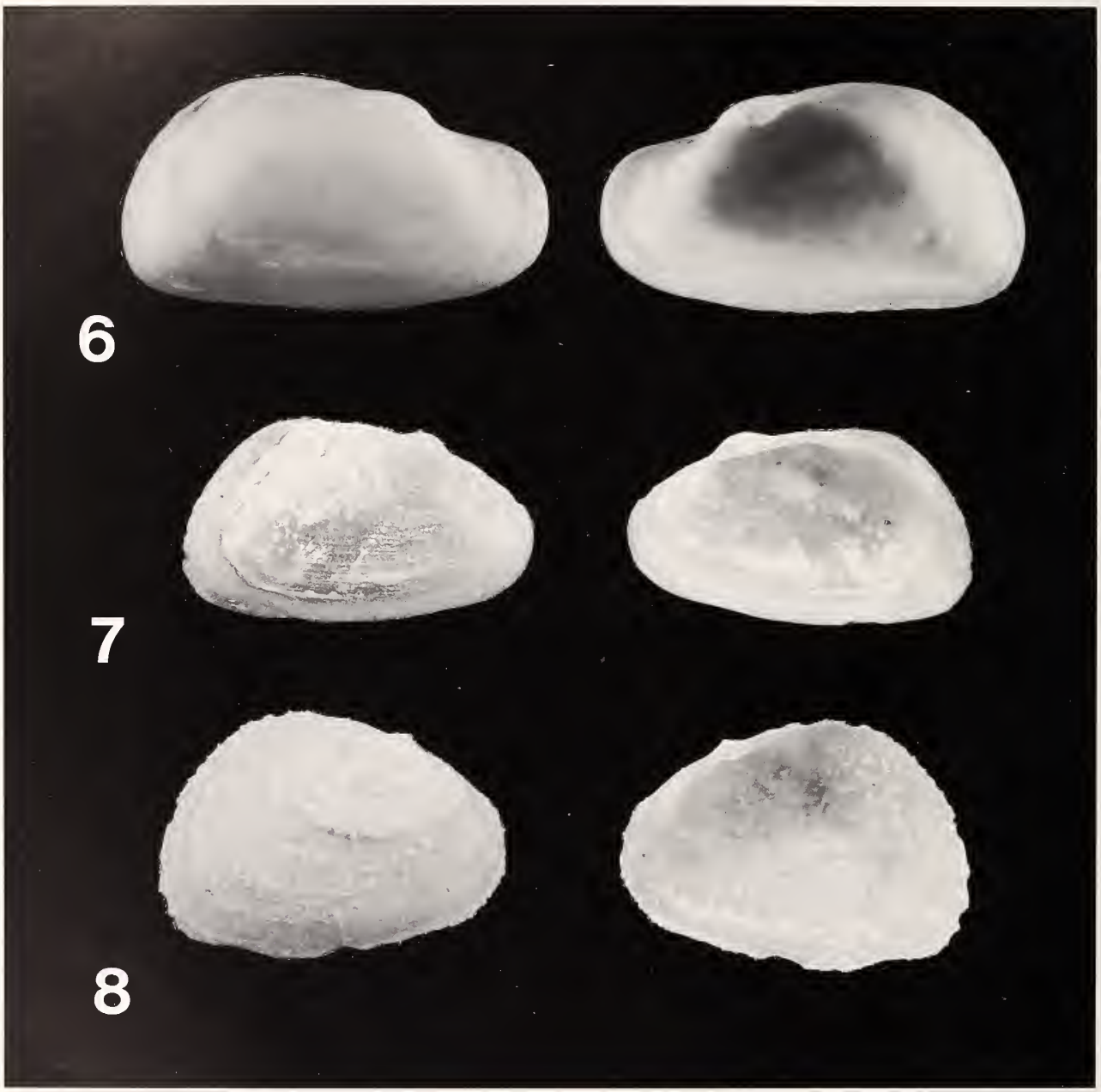
Reproductive Biology: Examination of histological sections has shown *Saxicavella* ***nybakkeni*** to be a simultaneous hermaphrodite that provides brood protection for its young. Embryos develop synchronously in a pouch posterior of the pedal gape. The pouch is formed between the fused inner mantle fold and the outer mantle fold (Figure 5). Embryos appear to be attached in the pouch by a byssus.

Brooding adults have been collected from April through July, but additional samples may show a longer or continuous breeding cycle. Up to 20 embryos have been found in a single brooding adult. Broods have not been detected inside the mantle cavity.

The method of embryo placement into the external brood pouch has not been discovered. It is highly probable, however, that the heel of the foot could easily provide a conduit from the mantle cavity, through the pedal gape to the external brood pouch.

DISCUSSION

Brood protection in bivalve mollusks is well documented and is found in more than 30 families (Sellmer, 1967; Mackie, 1984). The most common form of protection involves ovoviviparous incubation within the mantle cavity, generally within a suprabranchial chamber. Much less common is oviparous secondary brooding, whereby embryos are protected outside the parent. Two primary methods have been reported for secondary brooding: (1) initial incubation within the mantle cavity of the parent, with



Explanation of Figures 6 to 8

Figure 6. Lectotype **herein** of *Saxicavella jeffreysi* Winckworth, 1930; right valve (USNM 171581); length, 9.0 mm.

Figure 7. Holotype of *Saxicavella pacifica* Dall, 1916; right valve (USNM 209912); length, 5.5 mm.

Figure 8. Holotype of *Saxicavella sagrinata* Dall and Simpson, 1901; right valve (USNM 160063); length, 5.5 mm.

subsequent release and secondary incubation (often of dwarf males) external to the parent (Knudsen, 1961; Morton, 1972; Ó Foighil, 1985), and (2) by an invagination of the shell margin, as in the carditids *Milneria kelseyi* and *Thecalia concamerata* discussed by Yonge (1969).

In his description of the galeommatid, *Ephippodonta oedipus,* Morton (1976) reported protection of two dwarf males in two external pouches made in the enlarged, reflected middle fold of the mantle. The dwarf males attach to the periostracum of the female while residing in a hole in the overlying mantle. In like manner, females of *Chlamydoconcha orcutii* Dall, 1884, provide a deep pore in the

mantle (presumably in the middle fold) for a single dwarf male to reside, and subsequently produce spermatozoa and fertilize the host female (Morton, 1981). In both species, fertilized eggs are internally incubated in the female ctenidia.

Saxicavella ***nybakkeni*** thus represents the first report of non-sexual brood protection between the outer and middle folds of the mantle. While embryos have not been located within the mantle cavity, it can be postulated that fertilization takes place within the parent followed by incubation to a byssus bearing stage. Larvae then travel to the external mantle pouch and are later released as crawl-away juveniles.

There have been no previous records of larval protection in the Hiatelloidea. With a reproductive mode well outside the hiatelloid line, as well as extreme siphonal reduction, it is possible that members of the Saxicavellinae should receive full family status.

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